THE EFFECT OF COLOUR ON RESPONSE EXECUTION AND INHIBITION IN THE STOP-SIGNAL PARADIGM

SHAWN C. BLIZZARD

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ABSTRACT

Recent investigations have shown that smooth pursuit target selection is biased according to a hierarchy of red, green, yellow, and blue (e.g. red is always selected over green). This implies that colours higher on the hierarchy have greater attentional salience. Using the stop signal task, we conducted experiments in which go signal colour was manipulated (exps. 1 and 2) and in which stop signal colour was manipulated (exp. 3) to determine whether the hierarchy also applied to response execution and inhibition. When colour was either irrelevant (exp. 1) or relevant (exp. 2) to response execution there was no effect on reaction times or individual RT variance. When colour was relevant to response inhibition (exp. 3) estimated stop signal reaction times were significantly faster for red (~225ms) relative to green (~250ms) stop signals. This suggests that response inhibition, but not execution, networks are sensitive to differences in colour salience.

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CHAPTER 1: INTRODUCTION AND VISUAL PROCESSING

1.1 Introduction

Vision plays a key role in our ability to navigate our environment. The sheer volume of information afforded to us through vision, however, would be overwhelming without the attentional mechanisms that we use to compartmentalize and enhance parts of the visual world. Information fed-forward from sensory systems and feedback from higher cognitive areas interact to produce appropriate behavioural outputs. While we do this with relative ease, these interactions are highly complex. Something as simple as the colour of a stimulus can impact how quickly such a stimulus is processed and acted upon (for example, see: Lindsey et al., 2010; Tchernikov & Fallah 2010; Pomerleau et al., 2014). What follows will be an exploration of the effects that colour has upon our ability to execute a behaviour or countermand/inhibit an ongoing behavioural plan. These findings will provide us with better insight into selective attention, colour processing, and how they interact to affect behavioural control.

1.2 Visual Processing in the Retina

The various layers of the retina are responsible for the first steps of visual processing. Visual processing begins when photons being reflected from objects and surfaces strike receptor cells on the retina at the back of the eye. There are two types of receptor cells, rods and cones. The brain processes sensory information using electrical impulses through either graded potentials or action potentials. Because of this, the light entering the eye is transformed in a process known as phototransduction. This is done through a series of chemical cascades that begins when a photon strikes a pigmentation molecule known as rhodopsin.

Under dim lighting conditions rod cells are highly sensitive to small changes in illumination and are the primary driver of vision under low lighting conditions. Under brighter conditions, however, these cells fail to differentially respond to changes in illumination. Cone cells, on the other hand, are relatively insensitive to changes in overall lighting and, as such, allow us to see in detail under daylight conditions (Kandel et al. (eds.), 2013). Importantly for colour vision, cone cells are subdivided into three types which each respond maximally to short, medium or long wavelengths of light respectively. These cells are differentiated by differences in the morphology of the opsin portion of the rhodopsin molecule. The relative activation of the chemical cascades in these cells provides for our entire visible electromagnetic spectrum.

The information provided by the photoreceptor cells is then transmitted to retinal ganglion cells in a many-to-one manner via either the rod-bipolar cell, or one of several types of cone-bipolar cells. It is at this point that parallel on and off pathways begin to emerge. The receptive fields of bipolar cells are organized in an on-centre off-surround manner. The centre-surround nature of retinal visual information processing is thought to arise from the lateral inhibitory effects of horizontal cells which are located near the axon terminals of photoreceptor cells. Horizontal cells provide synaptic connections between photoreceptor cells and from photoreceptor cells to adjacent bipolar cells. On bipolar cells are most active when their corresponding rods or cones hyperpolarize (i.e. under light conditions) and, therefore, do not release glutamate. Off bipolar cells are most active when their corresponding rods or cones are depolarized (i.e. under dark conditions). Rod bipolar cells have no direct synaptic connection to ganglion cells but, rather, they connect to amacrine cells which in turn either excite or inhibit an on or off cone bipolar cell. Cone bipolar cells, on the other hand, can connect directly to the corresponding on or off ganglion cells but also synapse with amacrine cells. It is important to

note that here we begin seeing a distinction between what are called the parvocellular and magnocellular pathways. The parvocellular (P) bipolar cells transmit information from a single cone whereas the magnocellular (M) bipolar cells convey information from multiple cones. Because they transmit information from single cones P cells are important in the processing of colour information and also lead to smaller downstream receptive fields.

Ganglion cells represent the last step of retinal image processing before the information is sent to subcortical and cortical structures in the brain. As with bipolar cells, ganglion cells are divided into on and off. Each ganglion cell receives input from many bipolar cells. An important piece of information gathered through ganglion cell visual processing is changing illumination. On ganglion cells increase their firing rate when the centre of their receptive fields are illuminated. This same illumination causes off ganglion cells to decrease their firing rate. When the centre of the ganglion cell's receptive field is not illuminated, the inverse occurs. Given the on-centre off-surround nature of these cells, if light is input to both the centre and surround of the cell's receptive field, the change in the ganglion cell's firing rate will be weaker than if only the centre of the receptive field was illuminated. For off-centre on-surround cells, changes in firing rate are greatest when light is illuminating the surround of the receptive field and the centre remains dark. The interplay between the various centre-surround configurations may allow for better contrast or edge detection and, therefore, may help later neural processing regions to more readily extract object form information.

M cells respond more quickly and also deactivate more quickly than do P cells. This means that M cells can convey information quickly with higher temporal resolution but without much detail. P cells, on the other hand, have a sustained response and can encode greater detail owing to the smaller receptive fields of ganglion P cells. Unlike M cells, P cells have poor temporal

resolution due to their sustained responding. In some primates, there is a third class of cell called koniocellular (K). K cells appear to respond primarily to input coming from the short-wavelength sensitive cones (e.g. Pietersen et al., 2014) but also appear to respond to various other visual features (e.g. gratings; see Hendry & Reid, 2000 for review). They may also be involved in vision not mediated through the primary visual cortex (e.g. Schmid et al., 2010).

Colour processing at the P ganglion cell levels occurs through what is called the colour opponency process (Hurvich & Jameson, 1957). Red-green opponent cells respond according to the relative differences in input received from the medium and long wavelength sensitive cones. Blue-yellow opponent cells, on the other hand, respond according to the difference in input between the short wavelength cone and a combination of the medium and long wavelength cones.

Ganglion cell axons converge into the optic nerve and exit the back of the eye. The optic nerve then semi-decussates at the optic chiasm to form the two optic tracts. The optic nerve splits such that information from just over half of the visual field is conveyed to the opposite side of the brain (e.g. the information coming from the left visual hemifield in both eyes is transmitted to the right side of the brain).

1.3 Visual Processing in the LGN and Cortex

The axons of the optic tract extend to the six layers (i.e. laminae) of the lateral geniculate nucleus (LGN) according to the cell type which projects the axon. The LGN is located in the midbrain and is considered part of the thalamus. The magnocellular ganglion axons project to laminae 1 and 2 while the parvocellular axons project to 3, 4, 5 and 6. The koniocellular axons project to layers intermediate to the others. As in the retina, information in the LGN is

represented using circular receptive fields. From here, information is conveyed via the optic radiations (i.e. the geniculostriate pathway) to the primary visual cortex.

The first stage of visual cortical processing takes place in the six layered primary visual cortex (V1). The primary visual cortex is located at the most posterior region of the occipital lobe and in the calcarine fissure. Visual information enters V1 from the LGN through layer 4 with some information also projecting to layer 6. Evidence from macaque monkeys shows that parvocellular information is sent to sub-lamina 4Cβ and then to layers 2 and 3 of the cortex (Tootell, Silverman, Hamilton, De Valois, & Switkes, 1988) while magnocellular information is sent to 4Cα, 4B and layer 6 (Tootell, Hamilton, & Switkes 1988).

V1 is organized in a retinotopic manner. This means that the spatial arrangement of light falling on the retina is preserved in V1. Unlike in the retina and LGN, however, neurons in V1 are selective for oriented bars as opposed to simple spots of light (Hubel & Wiesel, 1959; Hubel & Wiesel, 1968). This is owing to their rectangular as opposed to circular receptive fields.

V1 is also organized into columns which are comprised of neurons which perform similar functions (e.g. encoding a particular orientation). This organization is further subdivided into what are called ocular dominance columns. These are comprised of neurons which correspond to information coming from each eye respectively (Hubel & Wiesel, 1969).

Beginning in early visual cortex, visual processing is split into two processing streams, ventral and dorsal. Processing occurs in a hierarchical fashion with early cortical regions representing low-level local information and later areas representing increasingly complex information. This eventually leads to whole object and scene representations at the latest stages of visual processing and allows for object recognition.

Ventral Visual Processing Stream

The ventral visual stream processes information conveyed by parvocellular cells such as form and colour. Colour information is processed by neurons which form clusters called blobs (e.g. Wong-Riley, 1979; Livingstone & Hubel, 1988; Conway, 2001) located in the upper layers of the primary visual cortex. These neurons respond to colour information regardless of changes in contrast luminance (e.g. Solomon & Lennie, 2005). As with retinal ganglion cells and in the LGN, blob neurons respond in a colour opponent manner. For the ventral stream, inter-blob space is comprised of neurons which respond selectively and maximally to a particular line orientations which arise from object edges, bars of light, gratings, et cetera (Hubel & Wiesel, 1968). It is important to note that these orientation selective neurons do not respond according to object identity but, rather, to local stimulus information.

From V1, orientation and colour information is sent to the interstripes and thin stripes of V2 respectively. The colour responsiveness of V2 thin stripes is similar to that found in V1. The neurons in the interstripes, however, now respond to orientation information defined by illusory edges (e.g. von der Heydt, Peterhans, & Baumgartner, 1984; Lee & Nguyen, 2001). Colour information from V2 is fed into the colour "globs" of V4 (Conway, Moeller, & Tsao, 2007). Evidence suggests that this is the first stage of processing in which perceived and not physical colour is coded (e.g. Schein & Desimone, 1990). In the interglob space, V4 neurons combine spatially contiguous orientation information from V1 and V2 to represent angles and curves (e.g. Pasupathy & Connor 2001; Girard, Lomber, & Bullier 2002; Gustavsen & Gallant 2003). Analogous to some V2 neurons, a subset of V4 neurons also respond to illusory contours which are defined by contrasting moving surfaces (for example, an object comprised of moving dots superimposed over a background field of dots which move orthogonal to the direction of those

comprising the object will elicit the percept of a segregated object and background; e.g. Mysore, et al., 2006; Larsson, Heeger, & Landy, 2010).

From V4, ventral stream information is sent to the inferior temporal cortex (IT). Here, receptive fields are much larger than in previous visual areas with some neurons having receptive fields which extend beyond the midline of the visual field (e.g. Gross, Rocha-Miranda, & Bender, 1972). This part of the cortex is often separated into posterior (PIT) and anterior (AIT) portions owing to the functional differences between neurons in these two locations (e.g. Kobatake & Tanaka, 1994). PIT neurons represent simple shapes presumably by combining the contour and angle information from V4. AIT neurons, on the other hand, respond primarily to complex shapes and particular objects (e.g. Gross, Rocha-Miranda, & Bender, 1972; Desimone & Gross, 1979; Kobatake & Tanaka, 1994). Damage to particular areas of the inferior temporal cortex can lead to profound behavioural deficits known as visual agnosias. Lesions to PIT result in apperceptive agnosia which is the inability to copy or match complex visual stimuli (e.g. drawing a circle or a letter) with preserved object identification abilities. Lesions to AIT result in associative agnosia which is the inability to properly identify the identity or function of an object (e.g. reporting that an object is a ring and that it should be placed on a finger) with preserved copying abilities (Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2013). Damage to an area known as the fusiform gyrus (also known as the fusiform face area) can result in prosopagnosia which is the inability to recognize faces or their proper configuration (e.g. Barton, Press, Keenan, & O'Connor, 2002; Damasio, Damasio, & Van Hoesen, 1982)

From here, ventral stream information is sent to areas which are thought to be responsible for higher level cognitive functions such as the prefrontal cortex for working memory and object

categorization (e.g. Chavis & Pandya, 1976; Ungerleider, Courtney, & Haxby, 1998; Ungerleider, Gaffan, & Pelak, 1989; Freedman, Riesenhuber, Poggio, & Miller, 2003).

Dorsal Visual Processing Stream

Dorsal stream neurons process information conveyed by magnocellular cells and encode things such as motion speed, direction and temporal frequency. As will be discussed in greater detail later, the dorsal pathway, in concert with the frontal cortex, is also heavily involved in the control of visual attention. From V1, information about local direction of motion represented by complex cells is sent to the thick stripes of V2 (Hubel & Wiesel, 1968; Movshon & Newsome, 1996). This information is eventually fed forward into the middle temporal area (area MT) and later to the medial superior temporal area (area MST). Neurons in area MT appear to encode information about both local (e.g. separate edges) and global (e.g. whole object) two-dimensional stimulus motion (Albright, 1984; Born & Tootell, 1992; Dobkins, Stoner, & Albright, 1998; Maunsell & Van Essen, 1983). There is also evidence that neurons representing global motion direction are located in visual area V3 (e.g. Braddick et al., 2001) which is a putative visual processing area prior to area MT. This information is built upon to represent more complex three-dimensional object motion representations in area MST. The dorsal portion of MST is sensitive to stimulus rotation, expansion and contraction, global direction information and spiral motion (Graziano, Andersen, & Snowden, 1994; Mineault, Khawaja, Butts, & Pack, 2012; Tanaka & Saito, 1989; Wall, Lingnau, Ashida, & Smith, 2008). There is also evidence that MST integrates information about self-motion (e.g. head and eye movement) presumably to help distinguish between self-motion and object-motion (Wiest et al., 2001). From here information is sent to the posterior regions of the parietal cortex where more complex motion information is represented (Raffi, Persiani, Piras, & Squatrito, 2014). Importantly for acting upon the visual

environment, the posterior parietal cortex has reciprocal connection with the prefrontal cortex and with various regions of the premotor cortex. These connections allow for the planning and updating of motor movement such as reaching and grasping (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; for reviews see: Goodale, 2011; Goodale, 2014) but are also involved in the planning and control of saccadic eye movements (Schiller & Tehovnik, 2005).

In summary, the visual processing system is hierarchical in nature with early areas representing simple stimuli (e.g. spots of light) and later areas progressively representing more complex information (e.g. whole objects and three-dimensional global object motion). Information pertaining to features such as form and colour are represented in the ventral visual pathway while information pertaining to motion (i.e. direction, speed, self versus object motion) is represented in the dorsal pathway. The encoding of this information, however, would not be useful if we did not have mechanisms in place which allow us to prioritize, remember, and act upon visual stimuli. The mechanisms underlying these behavioural functions are known as the executive functions.

CHAPTER 2: THE EXECUTIVE FUNCTIONS

The executive functions represent the highest levels of cognitive complexity and allow for us to act upon both internal information (e.g. behavioural goals) and external information (e.g. visual input). Working memory, attention, and motor-planning, -execution, -inhibition, and -updating all play key roles in the control of our behaviour.

2.1 Working Memory

Working memory refers to the storage and updating of information that is being used for current behavioural goals. It has traditionally been split into two types, verbal and visuo-spatial. Verbal working memory involves keeping vocal linguistic information in conscious awareness so that it may be used for an ongoing task (e.g. silently repeating a phone number). Cognitive psychologists have postulated that verbal working memory is broken down into two components, the phonological loop, which keeps the information "in mind", and the subvocal rehearsal system which is responsible for the "inner voice" of thought. Paulesu, Frith, and Frackowiak (1993) reported that the phonological loop appears to involve the left supramarginal gyrus (located just superior to the temporal cortex and rostral to the post-central gyrus in the parietal cortex) while the subvocal rehearsal system engages Broca's area. This region of the temporal cortex is also involved in the vocal production of speech.

As the name suggest, visuo-spatial working memory involves keeping features or objects, and their locations in mind for immediate action. Recent cognitive models postulate that there aren't separate networks for visual perception and visual working memory. Rather, it is theorized that spatial information is dynamically accessed from the parietal cortex while object identity and function information is accessed from the inferior temporal cortex with the prefrontal cortex acting as an executive controller of the process (for review see Zimmer, 2008). Interestingly, there is also evidence to suggest that visuo-spatial working memory is heavily influenced by visual attention (Chun & Nakayama, 2000; Chun, 2011; Theeuwes, Belopolsky, & Olivers, 2009; Theeuwes, Kramer, & Irwin, 2011).

2.2 Visual Attention

Through vision, we are afforded a plethora of information. The amount of information in the visual environment, however, would overwhelm visual processing and behavioural control systems without a mechanism to prioritize incoming information. To improve the efficiency of planning, decision making and cognitive resource allocation there is an executive function called selective attention. There are two subtypes of attention classified according to the direction of information flow, bottom-up and top-down. Bottom-up attention refers to when external stimulus characteristics drive the prioritization of the stimulus for further processing. An example of this would be the red flashing lights at a railroad level-crossing. In this case, they are meant to capture resources from the processing of other tasks to usher some change in behaviour. Top-down attention refers to when internal states (e.g. search goals, task instructions) drive the selection of external stimuli for further processing. This would occur, for example, when searching for a red pen on a disorganized desk. Red stimuli would be selected for further processing, making the search for the red pen more efficient. Both bottom-up and top-down attention can be further subdivided into spatial, object- and feature-based attention.

Spatial Attention

Spatial attention refers to the mechanism which prioritizes information processing for a particular spatial location. There are two primary types of spatial attention, covert and overt. Covert attention refers to when processing is enhanced for locations about the visual field without movement of the eyes. Overt attention, n refers to when this enhanced processing is moved about the spatial environment through reorienting movements (e.g. saccades, head

movements, body movements, etc.). In other words, preferential processing of stimuli can occur for locations both within and around the current locus of fixation.

A classic experiment using what is now known as the Posner cueing paradigm provides an intuitive example of the behavioural effects of covert bottom-up spatial attention (M. I. Posner, Snyder, & Davidson, 1980; M. I. Posner, 1980). In these experiments, participants are required to keep their eyes centrally fixated while a cue appears either to the left or to the right of fixation. Shortly after the cue disappears a target is then presented at either the same or the opposite location as the cue and participants must report the location of the target. If the target appears on the same side as that previously occupied by the cue participant response times are speeded relative to a no-cue condition. On the other hand, if the target appears in the opposite location reactions times are slowed. It is important to note that longer latencies typically result in slower responding even if the target appears in the location once held by the target (Posner, Rafal, Choate, & Vaughan, 1985). This is thought to be due to a mechanisms known as inhibition of return where attention to cued locations is disengaged so that other locations can be prioritized. Because attention must be reengaged at the previous location there is a reaction time cost (for review see Klein, 2000).

Recent neurophysiological evidence suggests that the effect of both overt and covert attentional deployment are more complex than a simple overall enhancement of neural responding for an attended stimulus if it happens to be placed within a neuron's receptive field. Lee and Maunsell (2010) showed that the maximal neural spike rate for MT neurons will always occur when a single stimulus moving in the neuron's preferred direction of motion is presented within the neuron's receptive field. If both the preferred and anti-preferred direction are presented at the same time within the neurons receptive field and overt attention is voluntarily

driven to the preferred stimulus (i.e. the subject saccades to the preferred stimulus), the spike rate is attenuated relative to the single preferred direction condition, however, it remains relatively constant over 200ms before attenuating. When using the same stimulus arrangement, if only covert attention is driven to the location of the preferred stimulus the spike rate initially rises to that which occurs for overt attending, however, the spike rate decreases more steadily over the following 200ms. If the non-preferred direction is overtly attended, the spike rate decrease is even more pronounced over the following 200ms. As expected if only the non-preferred direction is presented within the receptive field, the neurons maximum spike rate is substantially attenuated and responding decreases quite sharply in the following 200ms. Several earlier studies also showed this effect for neurons in V2, V4 and certain locations in area IT (e.g. Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985).

Object-based Attention

Object-based attention refers to the prioritization of processing for either parts (i.e. features or, in the case of three-dimensional object, surfaces) or the whole of an object. Object-based attention is often invoked by superimposing objects which vary along some feature dimension. This is done to account for the fact that separated objects can only occupy single locations in space which confounds spatial and object-based attention.

In an experiment reported by Blaser, Pylyshyn, and Holcombe (2000) participants were required to track, through feature space, a target gabor superimposed with a distractor gabor. Each gabor patch was cycled through various features dimensions such as direction of rotation, colour saturation, and spatial frequency of the stripes comprising the gabor. Each of the gabor patches cycled through these dimensions such that they were indistinguishable as two separate

objects for some of the time. Despite their superimposition and occasional overlap in feature space, participants were able to identify the target gabor with overwhelming accuracy. In a second experiment, participants were required to report a discontinuity in the cycle through feature space of two features, either within the same gabor patch or across two of them. If the results of their first experiment are due to object-based attention, then participant should be able to more accurately report the discontinuities if they occur on the same gabor relative to if they occur on separate patches. Indeed, average performance accuracy was 80% when the discontinuities occurred on a single gabor and accuracy decreased to an average of 69% when they occurred across both gabors. The results from these two experiment suggest that participants are able to attend to a particular object as a unitary percept and not simply because objects are typically segregated in space.

Neurophysiological evidence of object-based attention in area V4 can be found in Fallah, Stoner, and Reynolds (2007). In their experiments the objects were superimposed rotating circular surfaces comprised of dots with each surface rotating in opposite directions. They sampled responses from colour selective neurons in V4. In experiment one, there was a delay between the onset of the first surface and the second. This was done because sudden onsets tend to capture attention automatically and, therefore, could be used to manipulate which surface was attended. In this case, the researchers determined a neuron's preferred colour and recorded activity from the neuron when the preferred colour was presented first or after the onset delay. When the preferred colour was presented followed by the non-preferred colour there was a reduction in spike rate. When the opposite occurred, there was an increase in spike rate. To determine whether this reflected a priority for the delayed surface the research conducted a second and third experiment. In the second experiment the surfaces were first presented outside

of the neuron's receptive field and then moved in tandem into the receptive field. Despite first appearing outside of the neuron's receptive field, the spike rate advantage for when the preferred colour appeared following a delay still occurred when the surfaces were moved into the neuron's receptive field. Their third experiment involved having two sets of superimposed surfaces, two within and two outside of the neuron's receptive field. The delayed onset either occurred within or outside of the receptive with the other surfaces being presented at the same time. Consistent with object-based attentional modulation, the spike rate advantage for when the preferred colour was delayed only occurred for the surfaces presented within the neuron's receptive field. This shows that responding of V4 colour selective neurons can be modulated by object characteristics and not global feature based mechanisms. Otherwise there would have been advantage for the delay occurring both within and outside of the receptive field.

Feature-based Attention

Feature-based attention refers to the global prioritization of processing for stimuli which share certain feature characteristic. As mentioned earlier, an example of feature based attention would be when searching for a red pen among cluttered items on a disorganized desk. Owing to top-down attentional modulation, neural responses for long red stimuli would be enhanced relative the responding for objects which do not meet these characteristics.

Many studies have provided evidence for feature-based attentional modulation of neurophysiological responses (e.g. Treue & Martínez Trujillo, 1999) and behavioural performance (e.g. Tchernikov & Fallah, 2010). Treue and Martínez Trujillo (1999) conducted a study to determine whether neurons in area MT could respond differentially according to the featural locus of attention. Macaque monkeys were required to maintain fixation while a random

dot kinematogram (RDK) appeared either within our outside of an MT neurons receptive field. RDKs are surfaces comprised of dots which coherently move through a circular aperture. The RDK within the neuron's receptive field was also moving in that neuron's preferred direction while the RDK outside of the receptive field could either be moving in the preferred direction or in some other non-preferred direction. When subjects attended to the preferred direction outside of the receptive field the spike rate for the neuron increased by approximately 13% relative to when the monkey attended to the non-preferred direction. Further experimentation showed that this was the result of both enhancement of processing for the preferred direction and suppression of processing for the non-preferred direction.

Feature-based attentional modulation during search has also been reported. Bichot, Rossi, and Desimone (2005) trained monkeys to freely search for a target either based on colour or form according to a cue presented just prior to the beginning of the search. They then measured both single units and local field potentials (a measure of neural population activity) to determine the effect of feature-based attention on the responses of neurons which prefer a cued stimulus' features. They found that when the cue matched a neurons preferred feature, spiking in all neurons responding preferentially to that feature was enhanced. As expected, when the target stimulus enters these neurons' receptive fields, this increase in spiking is further enhanced even if the monkey has not yet finished their search for the target.

The feature-based modulation of neural responses has also been found in humans. Saenz, Buracas, and Boynton (2002) conducted a study similar to Treue and Martínez Trujillo (1999). In an fMRI participants were presented with two overlapping RDKs in one visual field while another appeared in the opposite visual field. The overlapping RDKs moved in opposite directions. Participants were told to attend to the direction of motion of one of the two

overlapping RDKs while ignoring the single RDK in the opposite location. To ensure that participants attended to the stimuli the RDKs speed would occasionally increase and participants were required to make a button response when this occurred. The researchers found increased BOLD activation in V1, V2, V3/V3A, and MT+ for the ignored stimulus when participants were attending to the overlapping RDK with the same direction of motion as the ignored stimulus.

These previous studies involved a top-down attentional component as the monkeys were trained to attend to a particular feature and human participants were given instruction for the locus of attention. A recent human psychophysics study by Tchernikov and Fallah (2010) investigated the effects of feature-based attention on smooth pursuit eye movements. Smooth pursuit is a reflexive action where a saccade to a moving target with sufficient speed with automatically lead to following the moving target with the eyes. In their first experiment participants were required to fixate while either a red, green, yellow or blue random dot kinematogram was presented in the lower quadrant of their peripheral vision either to the left or to the right of fixation. When the stimulus appeared participants were tasked with saccading to the RDK. The speed of automatic smooth pursuit was measured during the subsequent time period. Because participants were not cued to a particular colour prior to their saccade, this task primarily involves bottom-up attentional modulation. The smooth pursuit gain (i.e. the ratio of smooth pursuit speed to the speed of object motion) was found to follow a colour hierarchy. Gain was highest for the yellow RDK followed by red, green, and blue. In a second experiment, two uniquely coloured RDKs with motion of equal speed but in opposite were superimposed and presented in the same fashion as in the first experiment. In this case, the researchers were interested to see if colour could bias the selection of the target for smooth pursuit. If one of the RDKs was red participants almost always selected it for smooth pursuit over the other colours.

Overall, the ability of an RDK to capture attention when in competition with another RDK was found to roughly follow a hierarchy of red, green, yellow and blue. These findings show that automatic bottom-up feature based attention can affect higher level behavioural outcomes.

2.3 The Control of Motor Functions

Both visual working memory and the various forms of attention interact to aid us in selecting and remembering information from the visual world for immediate action. This leads to the final stages of executive functioning, the various facets of motor control. Through a variety of cortical and subcortical mechanisms that will be elucidated in this section, we are able to plan a movement, execute that plan, inhibit motor functions that are irrelevant to that plan, and update a plan. Updating can take the form of countermanding (i.e. the complete suppression of a planned or ongoing movement) or changing an ongoing motor plan in light of new information. For the purposes of this thesis, this section will focus primarily on the anatomical substrates of the control of simple motor responses (e.g. button presses) as opposed to more complex responses (e.g. reaching out to and manipulating a computer mouse).

Basal Ganglia: The Limbic, Associative, and Oculomotor Loops

The basal ganglia are a collection of subcortical structures responsible for a wide array of functions. On the basis of various motor disorders, mood disorders, addiction, and functional connectivity studies, the networks of the basal ganglia have been divided along several dimensions. Functionally, the basal ganglia can be divided into limbic, associative (i.e. cognitive), oculomotor, and skeletomotor networks. They can also be further divided into the direct, indirect, hyperdirect pathways.

The limbic networks are through to drive emotional responses and may also be involved in behavioural motivation (for a review see Buot & Yelnik, 2012). Indeed, there is evidence to suggest that the limbic networks in the basal ganglia are involved in schizophrenia (e.g. Csernansky, Murphy, & Faustman, 1991), depression and bipolar disorder (for a review see Ring & Serra-Mestres, 2002). This may provide a lower level explanation as to why certain motor disorders, such as Parkinson's disease, are often comorbid with mood disorders such as depression (Rickards, 2005).

The associative networks are involved in higher cognitive functions such as memory retrieval, problem solving and long-term goal planning, and social cognition, among other things. Associative networks can be subdivided according to their origins in the prefrontal cortex, the dorsolateral and lateral orbitofrontal regions. (for a review see Bonelli & Cummings, 2007).

The basal oculomotor system is involved in the execution and inhibition of eye movements. Along with the superior colliculus and the parietal cortex, targets for fixation are selected while distracting information and, therefore, competing motor plans are inhibited. The primary input to the basal ganglia for oculomotor control is from the frontal eye fields and the supplementary eye fields, located just anterior to the premotor and motor cortices (e.g. Berman et al., 1999; Bichot & Schall, 1999; Petit & Haxby 1999; Moore & Fallah, 2001).

The Corticobasal Control of Motor Execution and Inhibition

As with the other corticobasal circuits those for skeletomotor control can be divided into three main categories based on their functional connectivity, the direct, indirect, hyperdirect pathways. Figure 1 shows these circuits in a visual schematic. The direct pathway is primarily involved in the control of motor execution whereas the two latter circuits control motor inhibition.

The direct pathway of skeletomotor control begins in the frontal cortical decision making areas (e.g. dorsolateral prefrontal cortex) which send information to the primary motor cortex (M1), presupplementary motor area (pSMA), and premotor cortex (PMA). Excitatory information from these regions is fed into the putamen, a primarily inhibitory node of the basal ganglia. The putamen projects inhibitory axons to the globus pallidus pars interna (GPi) and the substantia nigra pars reticulata (SNr). Neurons comprising these areas project inhibitory axons to the appropriate nuclei of the thalamus. As they are receiving inhibitory input, the GPi and the SNr no longer inhibit the thalamus. This presumably allows for the release of an appropriate motor response through the excitatory effect of the thalamus on the motor cortices. Cortical information is then sent to the brain stem and spinal cord to provide signals to the skeletal muscle to perform an action.

In the indirect pathway, information is sent from decision making areas of the frontal cortical regions to the motor cortices. As in the direct pathway, this information enters the basal ganglia through the putamen. The putamen then projects inhibitory neurons to the globus pallidus pars externa (GPe), the counterpart to the GPi involved in the direct pathway. This results in the inhibition of the GPe, therefore, reducing the downstream inhibitory effects of GPe on STN. The STN projects excitatory axons to the GPi and the SNr. As mentioned before, these structures are inhibitory and project axons to the thalamus. Therefore, there is a net reduction in the excitatory activity sent from the ventrolateral thalamus to the motor cortices, resulting in reduced motor activity.

Recently, a faster hyperdirect pathway has been identified. In this pathway, information from the frontal cortices is fed directly into the STN. Excitatory neurons project from the STN to the GPi and SNr which then inhibit the thalamus. Owing to the direct connection between the cortex

and the STN, information travels faster through the hyperdirect pathway relative to the others (Nambu et al., 2000; Nambu, Tokuno, & Takada, 2002). A model by Nambu et al. (2000) posits that the hyperdirect pathway leads to a more global inhibition of all motor plans. Shortly after, through the direct pathway, the subset of actions required for the appropriate or intended motor plan are released.

Frontal Neural Correlates of Inhibitory Motor Control

Many studies of the motor control circuits use tasks which force an interaction between execution and inhibition, namely the stop-signal task and the go/no-go task. In the stop-signal task, subjects are required to make an accurate and rapid response to a go-signal but must countermand this response if a stop-signal is presented shortly afterward. Using various methods, researchers can estimate the stop-signal reaction time (i.e. how long it took to process and act upon the stop signal; SSRT) and use that to determine whether an area may be involved in the stopping process itself or some other post-stopping process. In the go/no-go task, subjects must respond or withhold a response according to the presentation of one signal, either a go- or no-go signal. Using these tasks, several recent studies have provided compelling evidence for the role of various frontal cortical areas in response inhibition and countermanding. Most recent models of response countermanding posit that the right inferior frontal gyrus (rIFG), M1 and the pSMA are the main sources (in the case of rIFG and pSMA) or are targets (in the case of M1) of inhibitory control information in the frontal cortex.

Mattia et al. (2012) recorded event related potential (ERP) signals from epilepsy patients who were temporarily fitted with subdural electrode grids over frontal brain areas including the motor cortices. ERP signals refer to the neural signals arising from specific sensory (e.g. visual

stimulus onset), motor (e.g. execution of a motor plan), and/or cognitive (e.g. visualization of visual information kept in memory) events. This particular methodology is known as electrocorticography (ECoG). The authors used a modified version of the traditional stop-signal task. In this case, trials began when participants placed their index finger at the location of a central cue presented on a display. On go-trials, the cue disappeared and a go-signal was presented either to its left or right. Participants were required to then move their finger to the location of the flanking stimulus. On stop-trials, the same would occur, however, the central cue would reappear after a variable delay. If the cue reappeared, participants needed to countermand the movement to the flanking go-signal. For successful stop trials, the researchers found a small negativity in the ERP waveform at approximately 200ms following the presentation of the central cue over M1, PMA, and the dorsal medial prefrontal cortex (dmPFC). Evidence suggests that the dmPFC may be involved in error prediction and cognitive control (e.g. Modirrousta & Fellows, 2008). This was followed by a large positivity at about 300ms. Following successful countermanding, waveform negativity once again appeared. Importantly, the majority of these waveform modulations occurred prior to the estimate of stop-signal reaction time. A similar pattern occurred for unsuccessful stop trials, however, the waveform was shifted later in time. As the sensory input is the same for both of these conditions, this suggests that M1 and PMA are necessary for successful response countermanding.

Another study using the stop-signal paradigm was conducted by Swann et al. (2009) to determine the potential contributions of the right inferior frontal gyrus (rIFG) and M1 on response countermanding. As in the previously described study, subjects were epilepsy patients fitted with subdural electrode grids. The task was similar to the traditional stop signal task with arrows serving as go-signals and an auditory tone serving as a stop-signal. For both successful

and unsuccessful stop-trials there was a significant increase in beta-power over the rIFG, however, the increase was greater for successful relative to unsuccessful stop-trials. These frequency band modulations occurred just before the estimated SSRT, suggesting that the rIFG is actively involved in the stopping process and does not simply index post-stopping response monitoring. Over M1, there was a significant decrease in both alpha- and beta-band frequencies for both successful and unsuccessful stop trials, however, the decrease was significantly smaller on successful stop trials. Because of the time course of their findings, the authors suggest that the rIFG is involved in the preparation and implementation of response countermanding and that M1 response frequency modulations are the downstream result of interactions between rIFG and the basal ganglia.

Another study was recently conducted by Fonken et al. (2016) which investigated the neural oscillatory effects of successful and unsuccessful response inhibition across prefrontal and motor areas. The researchers were primarily interested in the differential propagation of gamma and beta frequency waveforms. In this study, patients who were fitted with subdural electrodes performed a stop-signal task. Go-signals were comprised of white arrows pointing either right or left. In go-trials, participants responded by pressing a mouse button corresponding to the direction of the arrow. On stop-trials, the arrow turned red and participants were required to countermand their response. For the motor cortex, when participants were preparing their response there was a decrease in the beta frequency power with a corresponding increase in high gamma frequency power. This occurred for both successful go and unsuccessful stop trials suggesting that it is an index of motor preparation and execution. On successful stop trials there was an increase in beta power with a smaller increase in gamma power relative to the other behavioural outcomes. Interestingly, there was also a sharp gamma power increase over the

medial frontal gyrus (MFG) which occurred before the estimated stop-signal reaction time for both successful and unsuccessful stop trials. The authors suggest that this might reflect attention to the onset of the stop-signal. There was an increase in gamma following the motor response and this increase was greater for unsuccessful versus successful stop trials. The authors suggest that this may represent the role of the MFG as a post-error response monitor.

These studies show the crucial role of the rIFG, MFG, and the motor cortices for both the inhibition of planned motor movements and post-trial response monitoring. Recent evidence suggests that the rIFG may not only play a role in the outright stopping of a motor response, but also that it might allow for temporary pausing of a response (e.g. Wessel, Conner, Aron, & Tandon, 2013; for a review of rIFG functioning see Aron, Robbins, & Poldrack, 2014). Other studies have also shown that the right presupplementary motor area (pSMA) is necessary for motor inhibition. (e.g. Cai, George, Verbruggen, Chambers, & Aron, 2012).

CHAPTER 3: CURRENT INVESTIGATION AND HYPOTHESIS

3.1 The Attentional Colour Hierarchy

Through visual processing and the various facets of executive function, we are able to efficiently and effectively act upon our visual environment. As mentioned earlier, a recent investigation by Tchernikov and Fallah (2010) showed that different colours can have a differential effect on the speed of smooth pursuit eye movements and target selection. Specifically, the likelihood of selecting a target for smooth pursuit among competing stimuli followed a hierarchy of red, green, yellow, and blue. The authors attributed this finding to the differential strength of processing for different colours.

Lindsey et al. (2010) provided further evidence for the colour hierarchy by measuring the time it took to find a desaturated target among fully saturated distractors. In line with previous work on attentional distraction participants found the desaturated targets significantly faster than they found the fully saturated distractors. Critically for the colour hierarchy, they found that participants found red desaturated among saturated distractors more quickly than green, yellow and blue desaturated targets among their respective distractors.

While the specific neural mechanisms involved in the colour hierarchy have been mostly theoretical and based purely on human psychophysical performance, Pomerleau et al. (2014) analyzed waveform of event related potentials (ERP) as a way of determining the temporal dynamics of the effect. ERPs refer to the neural signals which propagate as a result of a visual stimulus onset. Their primary concern was with the onset time and magnitude of the N2PC, positive posterior contralateral (PPC) and positive temporal component (PTC) waveforms. The N2PC waveform has been described as an indication of spatial filtering or surround suppression (Steven J Luck & Hillyard, 1994), of target feature enhancement at an attended location (Mazza, Turatto, & Caramazza, 2009), and as an index of the localization of a target prior to the deployment of attention (Tan & Wyble, 2015). The PPC is a positive waveform with an onset located in the occipital cortex contralateral to the hemifield in which the stimulus was presented (e.g. if the stimulus was presented in the left hemifield then the PPC will appear for that stimulus in the right hemisphere of the occipital cortex). The PTC describes a positive waveform which occurs in the hemisphere contralateral to stimulus presentation much like the PPC, however, it is located in the temporal cortex.

Participants were asked to report the number of target stimuli in an array on a display according to the colour (either red, green, yellow or blue) of a circle in which the target was

located. The participants were presented with several arrays in succession and were told to count with speed in mind. Each array consisted of only one colour type. The counting was simply to ensure that participants were properly attending to the stimuli on the screen during ERP collection.

Pomerleau et al. (2014) found that the N2PC waveform appeared earliest for red stimuli (205ms) compared to blue (223ms), green (250ms) and yellow stimuli (253ms). There was no difference in the peak amplitude of the N2PC as a function of colour. The PPC waveform occurred earliest for blue stimuli (112ms), followed by red (130ms), green (149ms) and yellow (159ms). It's important to note that the difference between the blue and red PPC waveforms were not significant. The PPC had a greater peak amplitude for red than for blue or green but the same amplitude when compared to yellow. Further comparisons of red and yellow showed that the larger amplitude was spread over a wider area for red when compared to yellow, thus corroborating the colour hierarchy (Tchernikov and Fallah, 2010). Finally, the PTC waveform had a greater peak amplitude in response to red than for any other colour. Because no other colours elicited an amplitude that was significant different from zero the authors did not compare the time of onset between colours. Generally, these results suggest that red stimuli elicit both an earlier and greater response and that, especially with regards to the N2PC waveform, the behavioural effects of red cited earlier may be due to the preferential processing of the colour red.

From the behavioural studies (Tchernikov and Fallah, 2010; Lindsey et al., 2010) we can see that colour captures attention in a hierarchy of red, green, yellow and blue. As shown in Pomerleau et al. (2014), however, the timing effects are more ambiguous with red producing the earliest N2PC followed by blue and then green/yellow. These differences may come from

differential task demands. In Tchernikov and Fallah (2010) and Lindsey et al. (2010) subjects were required to make eye movements to targets and colour was a relevant target feature. In other words, responses for colour were made directly according to the stimuli being displayed. In Pomerleau et al. (2014) responses were made according to an arbitrary association between colour and target identity and so colour was not directly relevant. This is consistent with the fact that neurons in the prefrontal cortex can be selective for features or objects in a manner dependent on task relevance (Asaad, Rainer, & Miller, 2000).

This leads to the question for the current study. Since the colour red appears to have priority for processing, might the colour hierarchy have an effect on higher level executive functions like response execution and inhibition? To answer this, we employed the stop-signal task as it is could provide an elegant measure of the effects of colour on motor control.

3.2 The Stop-Signal Task

The stop signal task was used by Logan and Cowan (1984) in their seminal work on executive function as a way to test and synthesize the findings of studies on behavioural and cognitive control. In this task participants are required to respond when a particular signal is presented but must countermand or inhibit this response when they are presented with some stop-signal. In Logan and Cowan's (1984) study, participants were required to respond using two keys to discriminate between two potential go-signals. When an auditory stop signal was presented, participants were required to cancel an ongoing action (i.e. countermanding) or stop an action from beginning (i.e. inhibiting). They also varied the delay between go-signal onset and stop-signal onset (stop-signal delay, SSD) in order to calculate an estimation of the minimum time required to react to the stop-signal (stop-signal reaction time, SSRT). They described these

competing processes with the “horse-race model” of behavioural control. In this model, execution and inhibition are independent processes which compete to reach threshold. Whichever process wins this race determines the behavioural outcome. More recent studies have provided support for this model in various contexts (Hanes, Patterson and Schall, 1998; Kalanthroff et al., 2013; Gulberti et al., 2014).

In our experiments, we modified the classic stop-signal paradigm. In experiment 1, participants were presented with a red, green, or white go-signal arrow and were required to respond according to the direction of the arrow using arrow keys. If, however, they were subsequently presented with an auditory tone, participants were required to countermand their response. Experiment 2 was the same as experiment 1 except colour was now made relevant to responding. Instead of responding according to arrow direction they now had to respond according to the colour of the arrow using colour coded response buttons. In experiment 3, the go-signal was a white arrow and participants were required to respond as they did in experiment 1. If the white arrow changed to either red or green, however, participants were required to countermand their response.

3.3 Hypotheses

Since prefrontal neurons respond to stimuli in a task-relevant manner, the attentional effects of colour should be dependent on the executive process that is tied to a particular stimulus. Therefore, it was predicted that subjects would respond faster to the go-signal when it was red compared to green (experiments 1 and 2) but that countermanding would be faster if the stop-signal was red compared to green (experiment 3). It must be noted that the neurons in the prefrontal cortex are not responsive specifically to colour. Rather, we expect that if object

information is fed into the frontal cortex then the advantage of faster or stronger processing for red will be maintained even in the object representation.

FIGURE 1

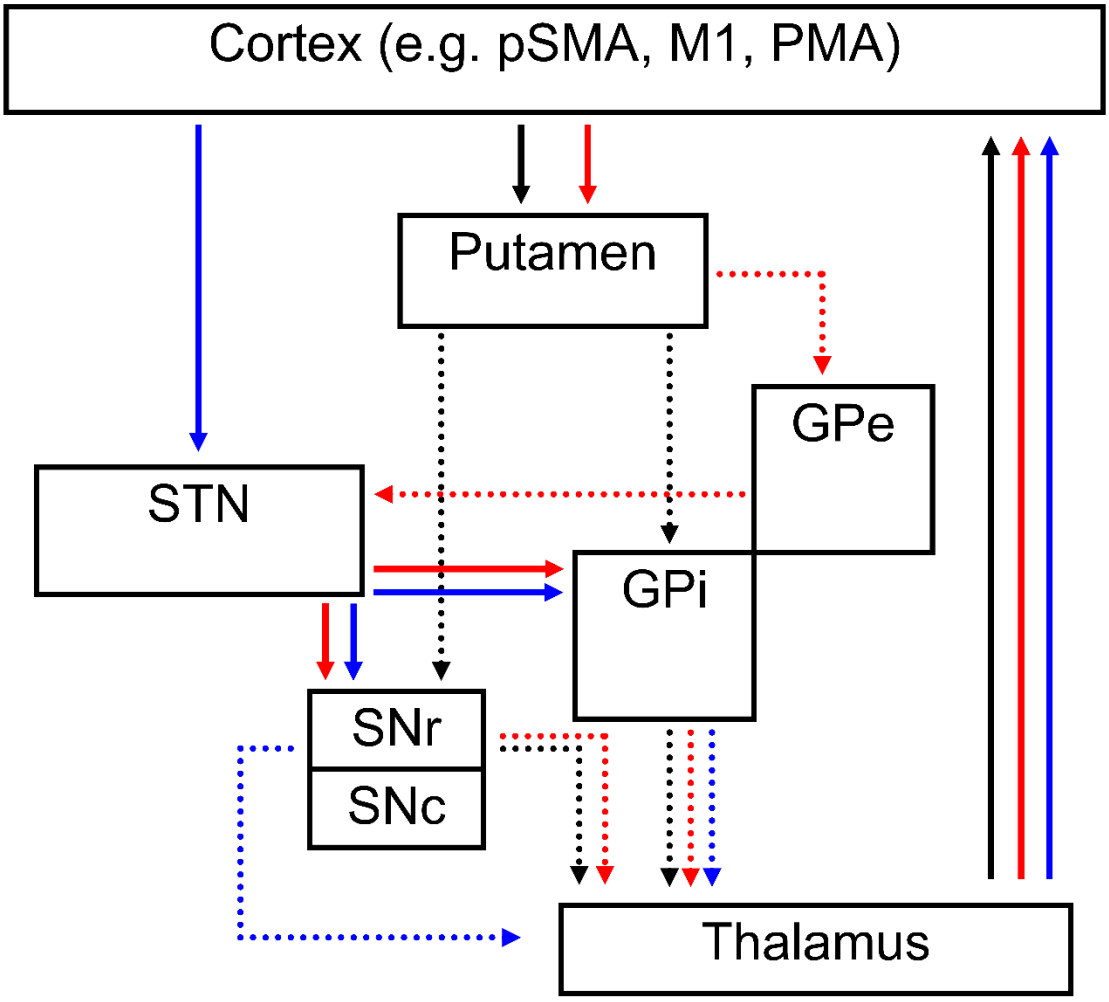

Figure 1: Schematic of the basal-ganglia circuits involved in skeletomotor control. Black lines represent the direct pathway, red lines represent the indirect pathway, and blue lines represent the hyperdirect pathway. Solid lines represent excitatory connections while dashed lines represent inhibitory connections. Note that the SNc has unrepresented dopaminergic connections with the putamen and other areas of the striatum. (*pSMA*: pre-supplementary motor area; *M1*: primary motor cortex; *PMA*: pre-motor area; *GPi*: globus pallidus pars interna; *GPe*: globus pallidus pars externa; *STN*: subthalamic nucleus; *SNr*: substantia nigra pars reticulata; *SNc*: substantia nigra pars compacta)

CHAPTER 4: MANUSCRIPT
In peer-review with Frontiers in Human Neuroscience

THE COLOR RED FACILITATES RESPONSE INHIBITION IN THE STOP SIGNAL PARADIGM

ABSTRACT

Actions are informed by the complex interactions of response execution and inhibition networks. These networks integrate sensory information with internal states and behavioural goals to produce an appropriate action or to update an ongoing action. Recent investigations have shown that, behaviorally, attention is captured through a hierarchy of colors. These studies, however, involved earlier processes involved in visual search and smooth pursuit target selection. To determine whether the colour hierarchy can be extended to higher level executive functions, we conducted several experiments using the stop-signal paradigm. In the first experiment, we modified the classic stop-signal paradigm so the go signals could vary in task-irrelevant colour, with an auditory stop signal. We found that the task-irrelevant colour of the go signals did not differentially affect response times. In the second experiment we determined that making the colour of the go signal relevant for response selection still did not affect reaction times and, thus, execution. In the third experiment, we modified the paradigm so the stop signal was a task relevant change in colour of the go signal. The mean reaction time to the red stop signal (stop signal reaction time, SSRT) was approximately 25ms faster than to the green stop signal. In other words, there was greater inhibitory control when presented with the red stimulus. Given that colour did not modulate response execution whether colour was relevant or not but did affect inhibition, we suggest that the colour hierarchy is based on attentional networks and not on early sensory processing.

INTRODUCTION

Our actions are generated by integrating sensory information into the response execution and inhibition networks. This produces a new action appropriate to the environment or takes an action which is already being carried out and updates or inhibits it. The prefrontal cortex works with the basal ganglia to control response selection and suppression (Mink, 1996; Gondo et al., 2000; Nambu et al., 2002; Chao et al., 2009; Hege et al., 2014; Jahfari et al., 2015; Rae et al., 2015).

Given that vision is a hallmark of the human experience it is not surprising that visual signals are used to usher, change or stop a particular behavior. For example, a traffic light turning red is designed to capture the attention of a driver and will, hopefully, bring about a swift movement of the foot from the accelerator to the brake pedal. However, if a driver is approaching a red light and it turns green, movement towards the brake pedal is countermanded and the foot stays on the gas. While there are certainly learned associations between colour and response selection there is evidence to suggest that the colour of a visual signal alone could alter its effectiveness (Tchernikov and Fallah, 2010; Lindsey et al., 2010; Pomerleau et al., 2014).

Tchernikov and Fallah (2010) measured smooth pursuit eye movements after subjects made a saccade to two superimposed moving random-dot-kinematograms (RDKs) segregated using colour. Smooth pursuit target selection depended on a colour hierarchy of red, green, yellow and blue which describes the inherent priority (salience) we give to the different colors. The velocity of pursuit was dependent on the difference in salience between the two objects. Thus colour intrinsically drives attentional capture and differences in intrinsic colour salience drive differences in motor output. Further support comes from Lindsey et al. (2010) where it was

found that target detection responses in a visual colour search task were fastest for warmer (i.e. redder) colors than for cooler (i.e. bluer) colors.

Electrophysiological evidence has also been found to complement these behavioral findings. In a study of event-related potentials (ERPs), Pomerleau et al. (2014) found that the N2PC waveform appeared earliest for red stimuli (205ms) compared to blue (223ms), green (250ms) and yellow stimuli (253ms). The N2PC has been described as an indication of spatial filtering or surround suppression (Luck and Hillyard, 1994), of target feature enhancement at an attended location (Mazza et al., 2009), and as an index of the localization of a target prior to the deployment of attention (Tan and Wyble, 2015). They also found that the PPC (positive posterior contralateral) waveform had greater amplitude for red than for blue or green but the same amplitude when compared to yellow. Further comparisons of red and yellow showed that the larger amplitude was spread over a wider area for red when compared to yellow, thus corroborating the colour hierarchy (Tchernikov and Fallah, 2010). Finally, the PTC (positive temporal component) waveform had greater positivity in response to red than for any other colour. The PTC, located over the temporal lobes, is thought to be an indication of activity in the ventral visual stream. These results suggest that red stimuli elicit both an earlier and greater response and that, especially with regards to the N2PC waveform, the behavioral effects of red cited above may be due to red being preferentially processed.

When comparing the four main colors these studies show evidence for a colour hierarchy of processing speed and strength. Behaviorally speaking, colors capture attention in a hierarchy of red, green, yellow and blue. The timing effects however were more ambiguous with red producing the earliest N2PC, followed by blue, and then green/yellow. It is possible that this difference may come from task demands. While in Tchernikov and Fallah (2010) and Lindsey et

al. (2010) subjects were required to make eye movements to targets and colour was a relevant part of the task, this was not the case in Pomerleau et al. (2014). Thus, colour salience effects on processing may be dependent on task demands, where the object is selected as a whole or colour is relevant to the response. This has important implications for behavioral execution and inhibition because it suggests that executive functions, which are dependent on sensory input, may also be faster for red signals than for those of other colors. In order to test this, we employed the stop-signal task as it provides an efficient way of measuring the interaction of colour salience with response execution and inhibition.

The stop-signal paradigm was used by Logan and Cowan (1984) as a way of synthesizing the vast amount of literature on both behavioral and cognitive control. In this task, participants are required to respond when presented with a go-signal but must countermand this response when presented with a stop-signal, e.g. pressing a button in response to a visual stimulus appearing and countermanding that response when an auditory tone was subsequently presented. Their findings provided support for what they called the "horse-race model" of behavioral control, also supported by more recent studies (Hanes et al., 1998; Kalanthroff et al., 2013; Gulberti et al., 2014). In this model, behavioral execution and inhibition are controlled by independent processes which compete to reach threshold. When one of the processes wins the race the other process is blocked from continuing. Response inhibition takes less time than response execution. So by varying the delay in presenting the stop signal after the go signal, the minimum amount of time needed for response inhibition can be determined.

Importantly for the present study, we predict that the attentional effects of colour should have an effect specific to the executive function tied to that stimulus. Thus, colored go-signals should affect response execution, but not inhibition, whereas colored stop-signals should affect

inhibition but not execution. This is because the two processes operate in parallel in the horse-race model that describes the stop-signal task. In other words, consistent with the colour hierarchy subjects should react more rapidly to red than other colors and this should either facilitate or impede response countermanding depending on the role of the red stimulus.

METHODS

Participants

All participants had either normal or corrected-to-normal vision and successfully passed Ishihara's Test for red-green colour blindness (Ishihara, 2006). Twenty-four student volunteers from York University completed experiments 1 and 3. The order that participants completed these experiments was counterbalanced. Of the 24 participants, 24 completed Experiment 1 (14 females, 10 males; ages 20-41) and 22 completed Experiment 3 (12 females, 10 males; ages 20-41). Three participants were excluded from data analysis for both experiments 1 and 3 due to poorer than chance performance on go-trials. The final analyses included the data from 19 participants (9 females, 10 males; ages 20-41). Thirty students from an introductory psychology course at York University completed experiment 2 (18 females and 12 males; ages 18-23). Each of these participants received partial course credit for their participation. Eight participants were excluded from data analysis due to poorer than chance performance on go-trials. As such, the data from 22 participants (14 females, 8 males; ages 18-23) were analyzed. In accordance with the Declaration of Helsinki all participants gave written informed consent prior to participation. All experiments were approved by York University's Human Participants Review Committee.

Equipment

Participants sat 57cm from an 18" CRT monitor (Dell M991, refresh rate = 60Hz, resolution = 1280x1024) with their head stabilized by a headrest (UHCO Tech). Experimental control was maintained by Presentation (Neurobehavioral Systems). For experiments 1 and 3, responses were made using left and right arrow keys on a keyboard. For experiment 2, responses were made using a serial response box comprised of colored buttons (RB-540 serial response box, Cedrus Corporation).

Stimuli and Procedure

Experiment 1

In this experiment we tested whether task irrelevant colour would affect response times. Specifically, we tested whether a red go-signal would improve response times when compared to a green or white go-signal. The go-signals were isoluminant red (CIE X = 46.8, Y = 24.52, Z = 2.75), green (CIE X = 12.02, Y = 24.42, Z = 4.42) and white (CIE X = 23.11, Y = 24.30, Z = 33.74) arrows. The stop-signal was an auditory tone (72dB, duration = 916ms).

Figure 1 (panel A) shows the time course of both stop- and go-trials in experiment 1. On all trials, an arrow randomly pointing either right or left was displayed at the center of the monitor. The arrow was pseudorandomly chosen to be isoluminant red, green or white. Participants were required to respond as fast as possible using the corresponding arrow key (go-trial). On a subset of trials (stop-trials) the arrow was followed by the auditory stop-signal and participants were required to withhold their response. Participants received visual feedback for errors on arrow

discrimination, responses on stop-trials and failures to respond within the 750ms time window on go-trials.

The delay between the go- and stop-signals (stop-signal delay, SSD) began at 50ms for each colour and then varied using a staircase design. Each block consisted of 6 go-trials and 3 stop-trials for each colour totaling in 27 trials per block. Trial type and go-signal colour were pseudorandomly interleaved within each block. Each time a participant was successful in countermanding their response on a stop-trial the SSD for that colour condition would increase, giving them less time for response inhibition on subsequent stop-trials. If they failed to countermand their response, the SSD would decrease, giving them more time for response inhibition on subsequent stop-trials. The step size of the SSD change started at 50ms for the first stage of the staircase. When performance on a stage reached a double reversal, the step size decreased for the next stage (20ms, 10ms and 5ms). The experiment ended after all stages were completed or when 102 stop-trials (34 blocks) were completed for each go-signal colour.

Experiment 2

In this experiment we tested whether task relevant colour would affect response times. The stimuli and procedure were the same as in experiment one except instead of responding according to the direction of the go-signal arrow participants were now required to respond with the button that corresponds to the colour of the arrow. They were instructed to ignore the direction of the arrow. Figure 1 (panel A) shows the time course of both go- and stop-trials for experiment 2.

Experiment 3

In this experiment, we tested whether the colour salience of a visual stop-signal would affect response inhibition, changing the time needed to countermand the response. The procedure was the same as Experiment 1 except for the following modifications. The go-signal arrows were always white and the auditory stop signal was replaced by an isoluminant colour change of the white arrow to either red or green. Each block consisted of 6 go-trials and 3 stop-trials for each stop colour condition totaling in 18 trials per block. Trial type and go-signal colour were pseudorandomly interleaved within each block and the SSD for each colour varied according to the same staircase procedure as in Experiment 1. Figure 1 (panel B) shows the time course of both stop- and go-trials in Experiment 3.

Data Analysis

Experiments 1 and 2

The first block for each colour was a practice block and the data was excluded from analysis. Response times which fell outside of +/- 2.5 standard deviations were removed from further analysis. Mean RTs were calculated as the average response time on go-trials for each go-signal colour. End RTs were calculated as the average response time on the final 8 trials for each go-signal colour. Final SSDs were taken from the stop-signal delay for each colour condition at the end of the session. SSRTs were calculated by subtracting the Final SSDs from the End RTs. Individual coefficients of variance (ICOVs) were calculated separately for each go-signal colour as the standard deviation of response times divided by the mean response times for that participant. Repeated measures ANOVAs, with go-signal colour as the independent variable,

were conducted separately for mean response times (RT), mean ICOVs, and stop-signal reaction times (SSRT).

Experiment 3

A repeated measures paired t-test with stop-signal colour as the independent variable was conducted for SSRTs. Because there was only one go-signal colour, mean RTs and ICOVs were not submitted to statistical testing.

RESULTS

Figure 2 (panel A) shows the response measures for Experiment 1. In Experiment 1, irrelevant go-signal colors produced no significant difference for any of the metrics: mean RTs ($F(2,36) = 1.94$, $p = .159$, $\eta 2p = .097$), mean ICOVs ($F(2,36) = 1.48$, $p = .240$, $\eta 2p = .076$), or SSRTs ($F(2,36) = 1.19$, $p = .317$, $\eta 2p = .062$). Paired t-tests for the a priori predictions revealed no significant differences between red and green go signals for any of the measures: mean RTs ($t(18) = 1.49$, $p = .155$, $dRM = .358$), mean ICOVs ($t(18) = -.011$, $p = .991$, $dRM < .003$), or SSRTs ($t(18) = 1.25$, $p = .229$, $dRM = .286$).

Figure 2 (panel B) shows the response measures for Experiment 2. In Experiment 2, relevant go-signal colors also failed to produce a significant difference for any of the metrics: mean RTs ($F(2,42) = 0.173$, $p = .841$, $\eta 2p = .008$), mean ICOVs ($F(2,42) = 0.395$, $p = .676$, $\eta 2p = .018$), or SSRTs ($F(2,42) = 1.456$, $p = .245$, $\eta 2p = .065$). Paired t-tests for the a priori predictions revealed no significant differences between red and green go signals for any of the measures: mean RTs ($t(21) = 0.494$, $p = .626$, $dRM = .107$), mean ICOVs ($t(21) = 0.839$, $p = .411$, $dRM = .179$), or SSRTs ($t(21) = -1.162$, $p = .122$, $dRM = .360$).

In Experiment 3, the stop-signal varied in colour but as the go signal did not, there was no test of colour on reaction times (Mean RTs and mean ICOVs). Figure 3 shows the SSRTs for Experiment 3. A paired t-test revealed that SSRTs were significantly faster (~25ms) for red stop-signals than green stop-signals ($t(18) = 2.17$, $p = 0.044$, $dRM = 0.498$). Effect sizes for paired t-tests (dRM) were calculated according to the method described in Morris & DeShon (2002).

DISCUSSION

In this study we were primarily interested in determining the relative effects of colour on behavioral execution and response inhibition, as measured in the stop-signal task. Previous investigations revealed a colour hierarchy of processing speed and strength with red stimuli producing faster and stronger processing than other colors (Lindsey et al., 2010; Pomerleau et al., 2014; Tchernikov & Fallah, 2010). According to the race model of executive function, the execution and cancellation of an action are independent processes which are in competition to reach threshold. Whichever process completes first determines the behavioral outcome (e.g. (Logan & Cowan, 1984). Combining the colour hierarchy and the race model, we found that colour, whether task irrelevant (Exp 1) or task relevant (Exp 2), did not affect response execution. However, task relevant colour did affect response inhibition as participants were 25ms faster to countermand their response when the stop signal was red versus green (Exp 3).

Taken together, these findings provide for further understanding of executive functioning in general and the nature of the colour hierarchy in particular. Faster search times, automatic target selection, greater pursuit gain, as well as stronger and faster propagation of ERPs for red stimuli relative to others can be explained by early biases in visual processing. The retina has a greater proportion of red cones than green or blue (e.g. Kuchenbecker et al., 2008). Thus there are more

neural responses to red through the early visual system. Our findings suggest that this cannot be the only mechanism underlying the attention effects of colour as this mechanism would result in facilitation for response execution as well as for response inhibition when comparing red to green. We propose that colour is preferentially processed by neural circuits underlying response inhibition.

These results appear to contradict prior studies, as we did not find effects of colour on response execution. Differences in task demands, however, explain this discrepancy. For example, in Lindsey et al. (2010) participants searched for red targets among distractors while in our study participants responded to a lone target. In other words, with competing stimuli, the attentional advantage for red results in more efficient search. This explanation is consistent with Pomerleau et al. (2014) who found that the N2PC waveform appears earlier and with greater amplitude for red compared to the other colors. The N2PC is an index of spatial filtering or surround suppression (Luck & Hillyard, 1994), of target feature enhancement at an attended location (Mazza, Turatto, & Caramazza, 2009), and as an index of the localization of a target prior to the deployment of attention (Tan & Wyble, 2015). Without competing stimuli, spatial filtering or surround suppression is not needed and so the speed of response execution would remain constant across colors. Conversely, spatial filtering or surround suppression cannot explain the effects on response inhibition determined by a colour change. Therefore, the effects on response inhibition likely result from a mechanism not indexed by the N2PC.

Putative Mechanism

The effect of colour on response inhibition but not execution likely arises from the differential propagation of signals through separate neural pathways. In the horse-race model, Logan and

Cowan (1984) posited that execution and inhibition are separate processes which race to reach some threshold. Whichever process reaches threshold first wins the race and determines the behavioral outcome. Recent neurophysiological work has provided physical evidence for functionally distinct but interacting subcortical (i.e. basal ganglia) pathways for starting and stopping actions, termed the direct, indirect and hyperdirect pathways. The direct pathway facilitates behavioral execution by inhibiting the effects of the substantia nigra pars reticulata (SNr) on the thalamus. This allows for voluntary movements to be released and executed through thalamic excitation of the motor cortex (e.g. Albin, Young, & Penney,1989). This pathway was not affected by task-relevant or irrelevant colour (Exps. 1 & 2). The indirect pathway involves inhibition of the globus pallidus which leads to the SNr increasing inhibition of the motor output centres of the thalamus. This has the effect of inhibiting motor excitation and thus it facilitates behavioral inhibition. As the same basal ganglia are involved as for response execution, it is unlikely that colour could play a role in this pathway. However, a third 'hyperdirect pathway' has also been proposed (e.g. Nambu et al., 2002). In this pathway, excitatory prefrontal cortical input is fed directly into the subthalamic nucleus (STN) which brings about the excitation of the SNr and globus pallidus. This has the double effect of modulating cortical input to the basal ganglia while also inhibiting output from the thalamus to the motor cortex. The hyperdirect pathway is named as such because it includes a more direct pathway from the cortex to the STN but also because the interneuron cascade of events occurs more quickly. The fast action of the hyper-direct pathway might preserve the advantage for red, therefore resulting in better inhibitory control, while the direct pathway may not, resulting in no differential effect on behavioural execution time.

Functional Advantage

While the colour hierarchy was initially elucidated using red, green, yellow and blue stimuli, these experiments focused on red and green as these colours are often used in the execution or inhibition of an action (e.g. red meaning stop and green meaning go). The colour red, in particular, may have been developed for use as a stop-signal because it is often associated with danger, such as poisonous berries and frogs, the colour of blood, or changes in skin tone when someone is angry. In these situations, it would be advantageous to inhibit a current behaviour in order to perform an alternate action. Alternatively, as red and green have many modern associations (e.g. traffic lights, elevator panels, user interfaces), the effects of colour on response inhibition may have arisen from experience. In fact, the evolutionary and the experiential effects may both be in effect. Though it should be noted that if training were solely responsible for the colour effects, we should have found a reaction time advantage for green stimuli as they are typically used to bring about behavioural execution (e.g. traffic light). Further experiments are necessary to elucidate the underlying neural circuitry that we are proposing.

Conclusions

We have shown here for the first time that the colour hierarchy affects higher level motor decision making circuits. Interestingly, there is no differential effect of go-signal colour on response execution times. For response countermanding, however, stop-signal reaction times show that red signals allow for participant to countermand response execution an average of 25ms faster than green signals. This provides further evidence both for an automatic colour hierarchy and for the dissociation between execution and inhibition networks, where colour is preferentially processed by circuits underlying response inhibition. Importantly, our findings also

show that the colour hierarchy is not the result of biases in early visual processing but, rather, that it is likely due to higher level attentional networks.

FIGURE 1

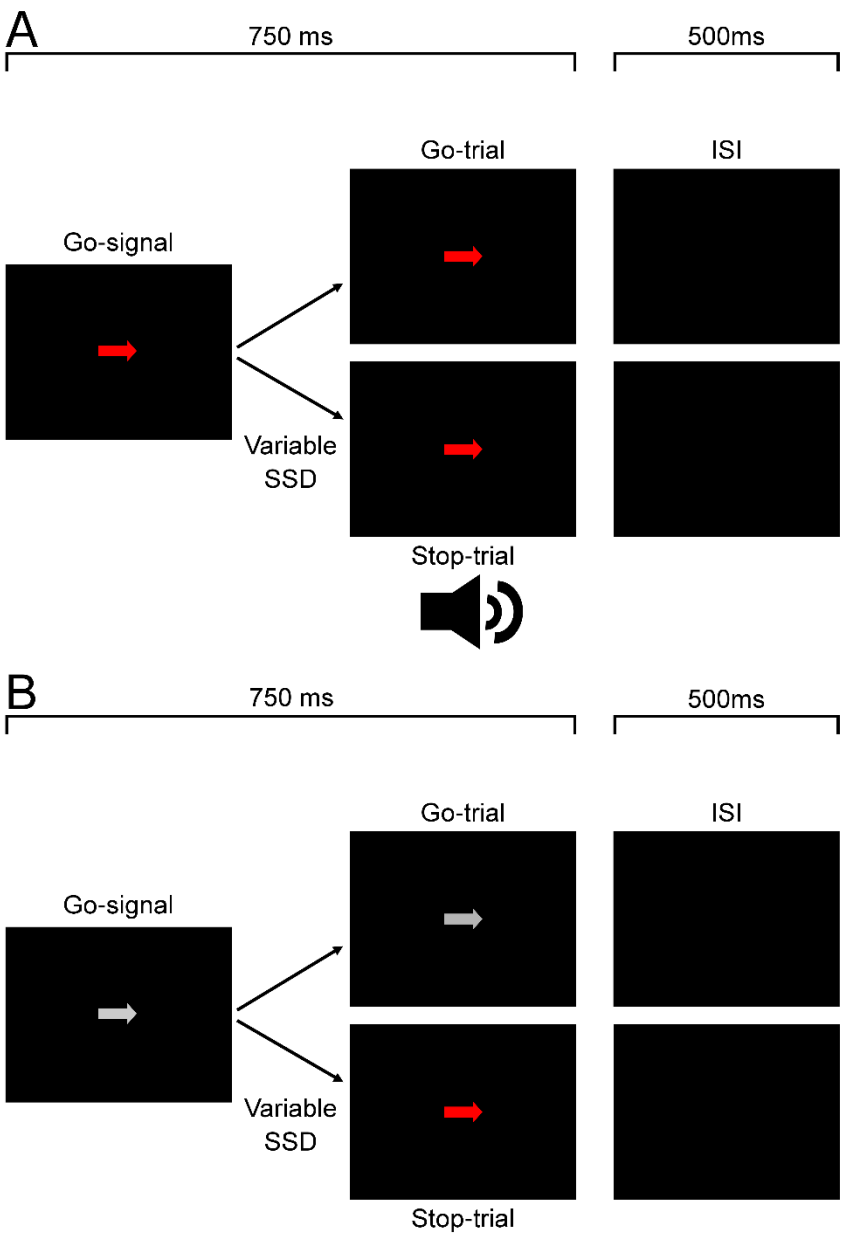
A
750 ms
500ms
Go-trial
ISI
Go-signal
Variable
SSD
Stop-trial
B
750 ms
500ms
Go-trial
ISI
Go-signal
Variable
SSD
Stop-trial

Figure 1: Time-course for trials in experiments 1, 2 (A) and 3 (B). In experiment 1, go signals were white, red, and green arrows pointing either right or left. On go trials participants were required to respond using an arrow key corresponding to direction of the go signal arrow. On 33% of trials, after a variable delay (SSD) an auditory stop signal was presented and participants were required to countermand their response. Experiment 2 was the same as experiment 1 except participants were required to make go signal responses according to the colour and not arrow direction. In experiment 3, the go signal was a white arrow pointing either right or left. On go trials, participants were required to respond according to the direction of the arrow. On 33% of trials, the white go signal would change to either red or green and participants were required to countermand their response.

FIGURE 2

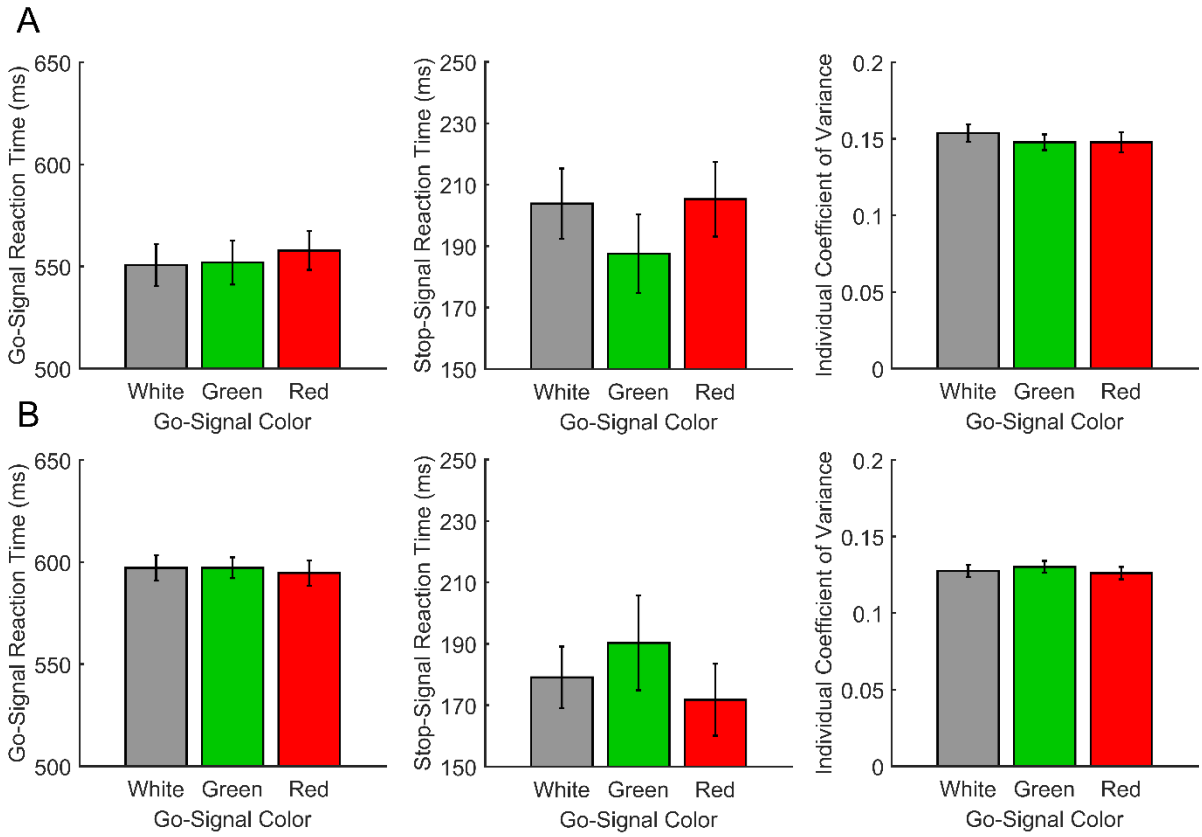

Figure 2: Response measures for experiments 1 (A) and 2 (B). From right-to-left, go signal reaction time (RT; ms), stop-signal reaction time (SSRT; ms) and the individual coefficient of variance (ICOV) are plotted against go signal colour.

FIGURE 3

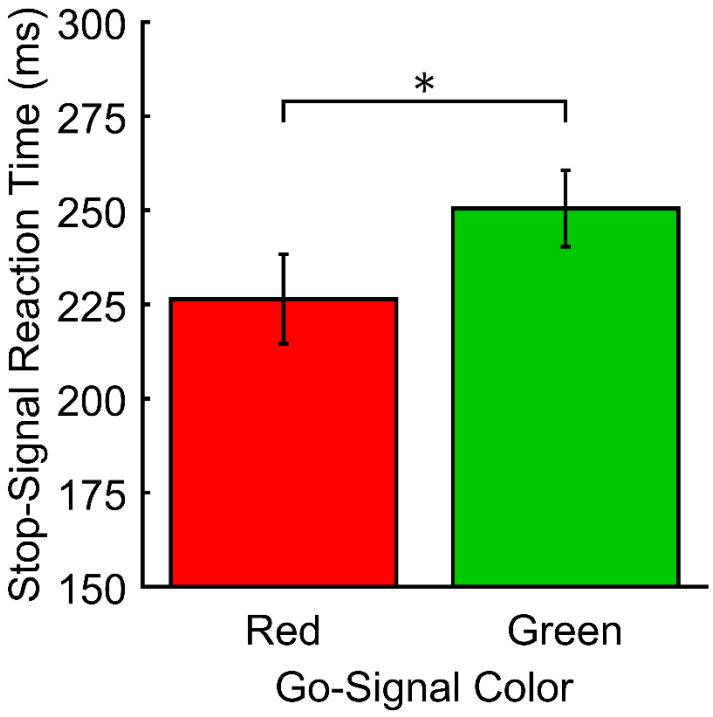

Figure 3. Response measure for experiment 3. Stop signal reaction time (SSRT; ms) plotted against go signal colour. * difference is significant at $p < .05$

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CHAPTER 5: GENERAL DISCUSSION

At its most basic, our goal in carrying out these three experiments was to further our understanding of the mechanisms that may underlie the attentional colour hierarchy first reported by Tchernikov and Fallah (2010). Specifically, we wanted to determine whether the colour hierarchy could be extended to the higher level executive functions which control motor responding and inhibition. To do this we used a modified version of the stop-signal paradigm. We found that regardless of the relevance of colour to responding, there was no differential effect of colour on response times. Interestingly, we did find that colour differentially affected response inhibition with stop-signal reaction times being an average of approximately 25ms faster for red go-signals versus green go-signals.

5.1 Potential Mechanisms

There are several possible explanations as to why inhibition, but not execution, was affected by the colour hierarchy. First, as discussed in chapter 3, there are dissociated pathways for execution and inhibition with further subdivisions theorized for the inhibitory control pathway. For execution, information is fed from the frontal decision making and motor areas to the putamen of the basal ganglia. The putamen has an inhibitory effect on the GPi which, in turn, allows for the STN/SNr to send excitatory signals to the ventral nuclei of the thalamus. The thalamus then sends information back to the motor cortices for relay to the brain steam and spinal cord. Since the colour of the go signal did not affect response execution time, the direct pathway is likely insensitive to colour differences.

For inhibition, there are two pathways through the basal ganglia, the indirect and hyperdirect pathways. The indirect pathway involves similar regions of the basal ganglia as in execution. Information from the putamen has an inhibitory effect on the GPe which, therefore, reduces the

effects of GPe on the STN. The STN sends excitatory efferents to the GPi/SNr which increases their inhibitory effects on the thalamus. This results in the inhibition of thalamic centres which would otherwise send information back to the cortex. As these two pathways involve similar structures, it does not seem likely that this would result in the differential effects of the colour hierarchy on response inhibition but not execution. Instead, the hyperdirect pathway may be responsible. In the hyperdirect pathway excitatory input from cortex bypasses the putamen and enters the basal ganglia through the STN. This increases the STN's excitatory effect on GPi/SNr, therefore, increasing the inhibitory effect of these structures on the thalamus. This results in the rapid inhibition of all information travelling back to the cortex. It is possible that the attentional advantage for processing the colour red is maintained when the salient stop-signal information enters the basal ganglia through the hyperdirect pathway, bypassing the putamen.

Another possibility may arise from the differences in stimulus presentation between the experiments where go signal colour was manipulated and the one in which stop signal colour was manipulated. In experiment 3, the stop signal was a change in the colour of the visual stimulus. Since the fronto-parietal attentional network is sensitive to sudden onset and is also comprised of regions necessary for updating behavioural plans in light of new information (e.g. Rushworth, Paus, & Sipila, 2001), the necessity for colour information to make the decision to countermand the response, integrates the colour hierarchy into the inhibitory control network. In the experiments where go-signal colour was manipulated, the sudden onset of the isoluminant arrow provides the same level of luminance onset activity within the dorsal stream. As such, the primary conduit for colour information to potentially modulate motor execution would have to come from parvocellular ventral stream information. But no such modulation was found,

suggesting that task-irrelevant colour information is not integrated into the response execution network.

On a behavioural level, there are several potential reasons why the visual processing and executive control systems have developed to result in our findings. For overall behavioural control, logically speaking, it is advantageous for current behaviours to be inhibited if new information suggests that a threat may be imminent. Specific to our findings and the colour hierarchy, it has been theorized that the colour red may be especially behavioural salient because of its associations with things such as blood, poisonous amphibians and berries, and changes in complexion signalling anger. Each of these can signal endangerment and so being able to react quickly and modify behaviour in light of these stimuli would be advantageous for the propagation of the species. There are also many modern associations between colour and response control. For example, red and green traffic lights are used to signal stopping and going respectively. Perhaps our findings are related to the learned associations between control and the meaning of these signals. To determine whether this is the case it will be necessary to extend the paradigm such that it includes the entire colour hierarchy. In other words, would there be a difference in response inhibition between colours that have differing strengths in the colour hierarchy but aren't part of the learned associations (e.g. orange and blue)?

5.2 Future Directions

Aside from including the entire colour hierarchy in future experiments it may also be worthwhile to perform ERP studies to better understand the potential temporal mechanisms behind the colour hierarchy and its effect on executive function. If the explanation of our findings can be found in the segregation of information between the dorsal and ventral visual processing streams, we would expect to see a differential time course for the propagation of

visually evoked potentials across colours between parietal and temporal portions of the scalp. Importantly, this would need to be done with colour as a task relevant feature in order to avoid the potential confounds discussed in the introduction regarding the findings in Pomerleau et al., (2014).

Another potential avenue for future study would be to determine whether the colour hierarchy applies to even higher level functions, such as post-response monitoring. A recent study by Beyer, Münte, Fischer, and Krämer (2012) looked at the neural oscillatory correlates of post-error slowing in the stop-signal paradigm. Post-error slowing refers to the fact that response times are slower for trials immediately following trials in which an error occurred. In the stop-signal paradigm, this typically occurs when participants fail to countermand their response in a preceding stop-trial but not when there was a simple failure to respond in a preceding go-trial. Interestingly, post-error slowing appears to be greatest when the stimulus from a previous failed stop-trial is repeated in the subsequent trial. Behaviourally, this was confirmed by Beyer et al. (2012). For neural oscillations, the researchers found that there was a significant increase in alpha frequency activity over occipital cortex following failed stop-trials relative to successful go- or stop-trials. Over frontal cortex there was a significant increase in beta frequency activity following stop-errors relative to successful stop- and go-trials. Frontal beta activity, however, returned to baseline before the beginning of the next trial. This finding runs counter to previous work discussed in chapter 3 showing that beta oscillations might index motor inhibition over frontal motor cortices. As such, the authors suggest that the beta oscillatory effects of stop-signal errors may simply be an index of error monitoring itself and not simply a result of inhibition. For our purposes, it would be interesting to determine whether the salience of the red stop-signal errors would drive greater oscillatory error effects and greater post-error slowing relative to

green stop-signal errors. This would mean that the greater salience for red stimuli can carry over to future behaviours. If this were the case, it may mean that the information is maintained in the frontal cortex across trials or that the colour hierarchy can also affect the neural substrates for working memory.

5.3 Conclusions

We have shown here for the first time that the colour hierarchy first reported by Tchernikov and Fallah (2010) can also be applied to some but not all higher level executive functions. Specifically, there was no effect of colour on response execution but participants reacted to red stop signals faster than green stop signals, resulting in faster countermanding. Our findings show that the colour hierarchy is not simply the result of biases in processing in the retina and early visual cortex, but dependent on fronto-parietal attention networks. These results also provide further support for the dissociation between execution and inhibition circuits in the brain. Furthermore, they imply that the networks controlling response execution are relatively insensitive to differences in colour, while information about colour is integrated into the networks controlling response inhibition when it is relevant to countermanding. Further studies to determine whether learned associations between red/green and behavioural outcomes are responsible will be necessary to elucidate the mechanisms underlying our results.

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